

# Climate will increasingly determine post-fire tree regeneration success in low-elevation forests, Northern Rockies, USA

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**Abstract.** Climate change is expected to cause widespread shifts in the distribution and abundance of plant species through direct impacts on mortality, regeneration, and survival. At landscape scales, climate impacts will be strongly mediated by disturbances, such as wildfire, which catalyze shifts in species distributions through widespread mortality and by shaping the post-disturbance environment. We examined the potential for regional shifts in low-elevation tree species in response to wildfire and climate warming in low-elevation, dry mixed-conifer forests of the northern Rocky Mountains, USA. We analyzed interactions among climate and wildfire on post-fire tree seedling regeneration 5–13 yr post-fire at 177 sites burned in 21 large wildfires during two years with widespread regional burning. We used generalized additive mixed models to quantify how the density of Douglas-fir and ponderosa pine seedlings varied as a function of climate normals (30-yr mean temperature, precipitation, soil moisture, and evapotranspiration) and fire (tree survivorship, burn severity, and seed source availability). Mean summer temperature was the most important predictor of post-fire seedling densities for both ponderosa pine and Douglas-fir. Seed availability was also important in determining Douglas-fir regeneration. As mean summer temperature continues to increase, however, seed availability will become less important for determining post-fire regeneration. Above a mean summer temperature of 17°C, Douglas-fir regeneration is predicted to be minimal regardless of how close a seed source is to a site. The majority (82%) of our sampled sites are predicted to exceed a mean summer temperature of 17°C by mid-century, suggesting significant declines in seedling densities and potential forest loss. Our results highlight mechanisms linking climate change to shifts in the distribution of two widely dominant tree species in western North America. Under a warming climate, we expect post-fire tree regeneration in these low-elevation forests to become increasingly unsuccessful. Such widespread regeneration failures would have important implications for ecosystem processes and forest resilience, particularly as wildfires increase in response to climate warming.

**Key words:** burn severity; climate change; conifer regeneration; dry mixed-conifer forest; forest resilience; range shifts; Rocky Mountains; wildfire.

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## INTRODUCTION

Climate is a primary driver of vegetation patterns, shaping tree species composition from

local to global scales (Woodward 1987, Stephenson 1990). Consequently, the distribution of many forest species is projected to shift in response to ongoing and future climate warming

during the 21st century (Rehfeldt et al. 2008, Gonzalez et al. 2010). However, these changes will likely be mediated by complex interactions between climate and disturbances (Millar and Stephenson 2015).

In many temperate coniferous forests, disturbances, such as wildfire, play a critical role in forest development by affecting tree mortality and recruitment. Post-fire ecosystem recovery is dependent upon abundant tree regeneration, which in turn is largely governed by mechanisms linked to seed production and dispersal, and seedling establishment and survival (Johnstone et al. 2016). Within the footprint of an individual fire, the severity and spatial configurations of burned patches impact the availability of seeds by modifying the distance potential seeds have to disperse to reach a burned site (Greene and Johnson 2000, Savage and Mast 2005, Haire and McGarigal 2010). Depending on the life history traits of individual tree species, regeneration strategies, and the spatial heterogeneity of burning, regeneration patterns are often spatially variable (Donato et al. 2009, Haire and McGarigal 2010, Harvey et al. 2016, Kemp et al. 2016). Likewise, wildfires impact seedling establishment by modifying resource availability and the microclimate suitable for tree germination and survival (Ehle and Baker 2003, Schoennagel et al. 2011, Tepley et al. 2013). For example, fire creates patches of bare mineral soil, increases light and nutrient availability, and reduces competition from surrounding vegetation (York et al. 2003, Gray et al. 2005, Moghaddas et al. 2008). Even where opportunities exist for post-fire establishment, however, germination and survival require suitable post-fire climate conditions (Rother et al. 2015, Harvey et al. 2016, Stevens-Rumann et al. 2018).

Most species in dry temperate conifer forests of western North America evolved with frequent low- to moderate-severity fire and thus possess traits that facilitate post-fire recovery (Halofsky et al. 2011, but see Roccaforte et al. 2012, Savage et al. 2013, Kemp et al. 2016). However, the resilience of these forests to wildfires may be increasingly compromised as warmer post-fire conditions and more frequent large fires with large high-severity patches limit seed availability and seedling establishment (Chambers et al. 2016, Stevens-Rumann et al. 2018). In western North America,

increasingly warmer, drier spring and summer conditions over the past several decades have been linked to longer fire seasons and increased area burned in forested ecosystems (Jolly et al. 2015, Abatzoglou and Williams 2016, Westerling 2016). These strong linkages between annual climate and fire activity, also consistent over the past century (Morgan et al. 2008, Littell et al. 2009), suggest an increasing probability of more extensive fires in a warmer future (Westerling et al. 2011, Barbero et al. 2015). As fires become more extensive, they will likely catalyze ecosystem changes that would otherwise unfold over decades to centuries (Crausbay et al. 2017), through increased fire-induced tree mortality and decreased post-fire regeneration under warmer climate conditions.

To understand how climate and wildfire interact to influence post-fire regeneration and potential future forest vegetation, we used climate observations and burn severity metrics to statistically model ponderosa pine and Douglas-fir seedling density across 177 sites spanning low-elevation dry mixed-conifer forests in the U.S. northern Rocky Mountains. Specifically, we were interested in understanding how seedling regeneration in these forests varied with mean climate conditions and fire effects that impact seed availability, seed dispersal, and establishment. We hypothesized that seedling densities would be lowest at sites with higher water deficit and with lower post-fire seed availability. We applied our statistical model to identify thresholds governing post-fire seedling regeneration and highlight how these interactions may unfold under scenarios of future climate change to impact forest resilience to wildfires.

## METHODS

### Study area

Our study region encompasses the dry mixed-conifer forest zone of the U.S. northern Rocky Mountains, from north of the Snake River plain in Idaho to south of Glacier National Park in Montana (Fig. 1). Steep river valleys bisect the terrain throughout the study region, creating large elevation gradients with distinct vegetation communities on contrasting aspects. South-facing slopes, especially at low elevations, are predominately a mix of canyon grasslands dominated by Idaho fescue (*Festuca idahoensis* Elmer)

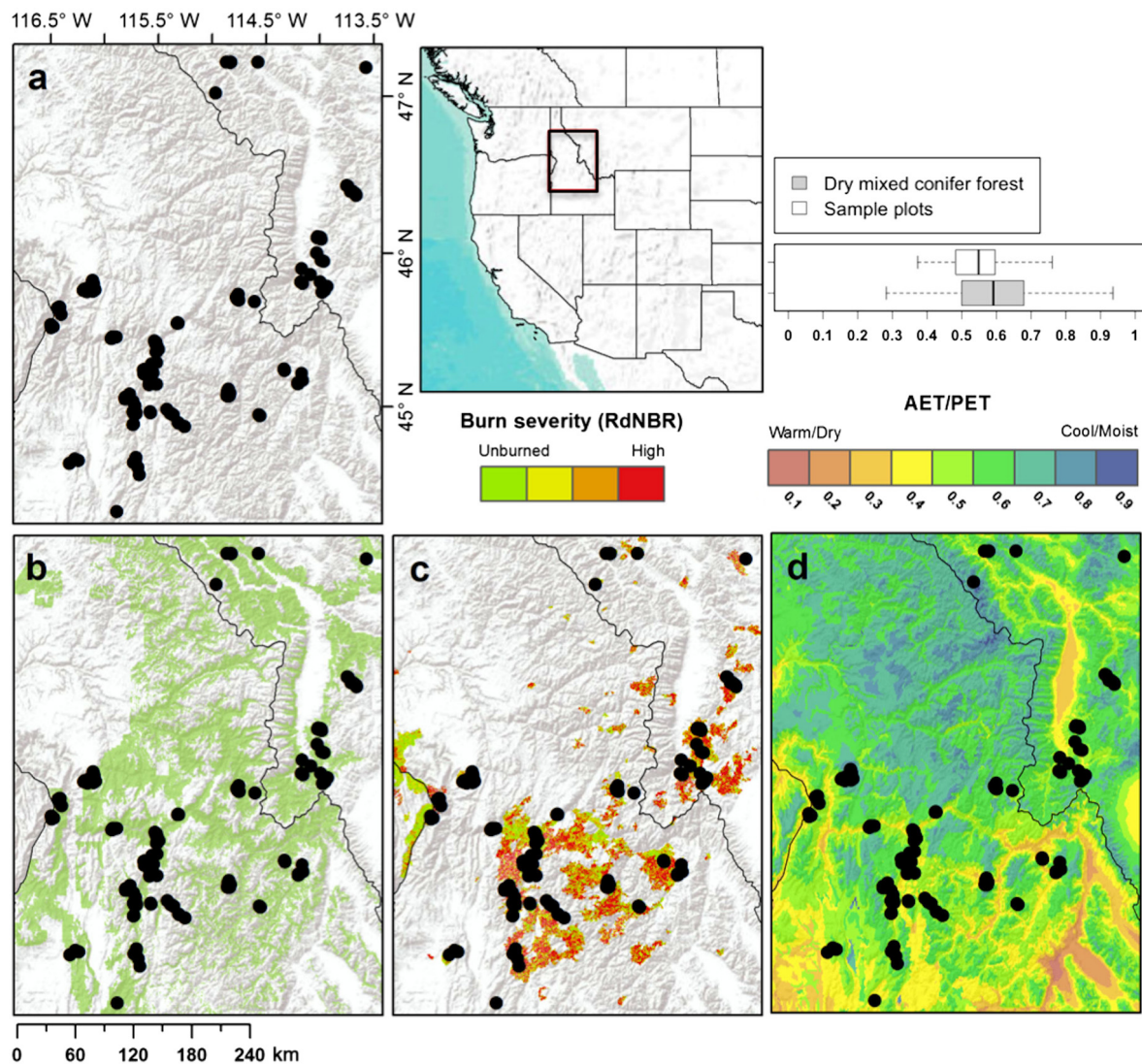


Fig. 1. (a) We sampled 177 sites across central Idaho and northwestern Montana in complex mountainous terrain that fell within (b) dry mixed-conifer forest type, (c) had burned in either 2000 or 2007, and that (d) represented a range of climate conditions characterizing the dry mixed-conifer forest vegetation type (defined here by the ratio of actual evapotranspiration to potential evapotranspiration [AET/PET]). Our sites were slightly biased toward lower-elevation warm dry sites across the range (boxplots). The AET/PET ranges from 0 to 1, where warm dry sites have a lower AET/PET ratio than cool moist sites.

and arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.) with sparse ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson). At higher elevations and on north-facing slopes, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), and lodgepole pine (*Pinus contorta* Douglas ex Loudon) dominate. The study region experiences dry

summers and wet winters. Observed average July temperature (1981–2010) across our study sites ranges from 12.0°C at high elevations (2203 m above sea level) in central Idaho to 22.4°C at low elevations in Hells Canyon (675 m). Average January temperature ranges from −7.0°C to −0.2°C, and total annual precipitation ranges from 450 to 842 mm. Soils are



predominantly coarse-textured inceptisols and entisols derived from granitic Idaho batholith parent material with limited soil water holding capacity (USDA 2014).

### Study design

We used a stratified random selection procedure to identify sites within low-elevation dry mixed-conifer forests, as classified from 30-m resolution LANDFIRE existing vegetation layers (LANDFIRE 2010), and which fell within four burn severity classes (unburned, low, moderate, and high severity, classified by the Monitoring Trends in Burn Severity product; Eidenshink et al. 2007) in 21 large (>400 ha) fires that burned in 2000 and 2007. Both 2000 and 2007 were years with exceptionally high fire danger and widespread regional burning (Morgan et al. 2014). The climatic conditions in these fire years approximate conditions projected to become more frequent with continued anthropogenic climate change (Barbero et al. 2015, Abatzoglou and Williams 2016). We inferred burn severity within each fire using relative differenced normalized burn ratios (Miller and Thode 2007) calculated by Dillon et al. (2011) from 30-m Landsat TM+ satellite imagery. We sampled 177 sites during the summers of 2012 and 2013 from the range of burn severity classes, on northeastern and southwestern aspects, and at low, mid, and high elevations (range: 675–2203 m). By stratifying site selection across a range of elevations and aspects, our sites span the climate range of dry mixed-conifer forests in the U.S. northern Rocky Mountains (Fig. 1).

Detailed field methods are described by Kemp et al. (2016) and summarized below. At each site, we counted live tree seedlings on a 60-m long transect that ranged from 1 to 10 m in width and was oriented perpendicular to the contour of the slope. The width of the transect on each site was determined prior to sampling based on an ocular estimate of tree seedling density; sampling effort was increased up to the maximum transect width to sample at least 30 seedlings of the most common species on each site. We also measured canopy cover and stand density of live and dead overstory trees at three locations along each transect, and the species and average distance to the ten nearest live seed trees from the transect center.

### Climate data

To represent the spatial variability in climate across our study region, we used a 30 arc-second (~800 m) resolution gridded climate surface of monthly temperature, precipitation, and dew-point temperature from the Parameter-elevation Regressions on Independent Slopes Model (PRISM Norm81; Daly et al. 2008) averaged for the period 1981–2010. Additional variables of wind speed and solar radiation needed for computing reference potential evapotranspiration (PET) using the Penman-Monteith equation (Allen et al. 1998) were acquired from the surface meteorological dataset of Abatzoglou (2013) with a 2.5 arc-minute (~4 km) resolution and bilinearly interpolated to the PRISM grid.

A modified Thornthwaite water balance model (Dobrowski et al. 2013) was used to estimate monthly mean actual evapotranspiration (AET) and soil moisture for the 1981–2010 baseline period. Actual evapotranspiration is a measure of the simultaneous amount of water available to plants and the energy demand on those plants from the environment (Stephenson 1990), which has proven useful in predicting tree species distributions in other studies (Lutz et al. 2010, Dobrowski et al. 2015) and should have potential to predict variability in seedling regeneration. For this type of water balance model, any water that is not stored in either the soil or snowpack, transpired by vegetation, or evaporated from the ground surface is considered runoff. The calculation requires information on latitude, mean monthly temperature, precipitation and PET, solar insolation, and available soil water holding capacity. We assumed a depth to restrictive soil layer of 150 cm (Stephenson 1990) and used available water storage data to estimate soil water holding capacity (STATSGO; Schwarz and Alexander 1995). Water deficit was defined as the difference between PET and AET and is a measure of drought stress on plants.

To model potential future seedling densities, we calculated differences in climate normals downscaled from climate projections from the fifth Coupled Model Intercomparison Project (CMIP5) between the historical (1971–2000) and mid-century (2041–2070) periods. We considered projections for climate model runs using the Representative Concentration Pathway (RCP) 8.5 experiment. Data were statistically downscaled

using the Multivariate Adaptive Constructed Analogs method (Abatzoglou and Brown 2012) to a 2.5 arc-minute (~4 km) resolution for 20 climate models (Appendix S1: Fig. S1). Given our interest in examining changes in climate normals, we calculated monthly averages in maximum and minimum temperature, solar radiation, precipitation, wind speed, and humidity for historical and mid-21st century experiments and then calculated the difference in these variables averaged across the 20 models. Because the observed, historical data (from PRISM) were at a finer resolution (800 m) than the downscaled data (4 km), we spatially interpolated projected differences between downscaled data to match the resolution of the historical data. To account for the slight difference in temperature between the baseline periods of 1971–2000 (for climate model experiments) and 1981–2010 (for observations), we applied a correction factor of +0.15°C to the 1971–2000 climate projections, which roughly accounts for observed warming over the two different baseline periods. Monthly climate projections were run through the water balance model to generate layers of AET, soil moisture, and

water deficit compatible with contemporary estimates. We used climate data at voxels co-located with each of our 177 sample sites to quantify 30-yr normals of seasonal temperature, precipitation, AET, PET, soil moisture, and water deficit for each site (Table 1).

### Statistical analysis

We used generalized additive mixed models (GAMMs) with a negative binomial link function to explore the influence of climate and fire on post-fire seedling abundance of the two most common low-elevation mixed-conifer species in the U.S. northern Rockies: Douglas-fir and ponderosa pine. We chose GAMMs because we had no expectations of a linear relationship between predictor and response variables (e.g., seedling establishment varies nonlinearly with distance to seed source; Kemp et al. 2016), and we used a negative binomial link function to directly model seedling counts, the raw data collected at each site. Seedling count was modeled as a function of a suite of derived temperature, precipitation, and water balance variables related to growing season conditions with mechanistic links to seedling germination and establishment,

Table 1. Description of explanatory variables considered in generalized additive models for predicting post-fire seedling abundance.

Process	Category	Variable	Description
Climate†	Temperature	Summer temperature (°C)	Average June through September temperature
		Seasonality (°C)	Difference between maximum summer temperature and minimum winter temperature
	Water balance	AET (mm)	Annual actual evapotranspiration
		AET/PET	Ratio of annual actual evapotranspiration to annual potential evapotranspiration
		Water deficit (mm)	Annual water deficit, calculated as the annual potential evapotranspiration minus annual actual evapotranspiration
	Precipitation	Soil moisture (mm)	Mean summer (June–September) soil moisture
		Spring precipitation (mm)	Total March through May precipitation
		Summer precipitation (mm)	Total June through September precipitation
Fire	Canopy cover	Canopy cover (%)	Canopy cover measured using a spherical densiometer; averaged from three locations on each transect
		Live tree stand density (trees/ha)	Density of live trees measured using a 2 or 4 m basal area factor prism post-fire; averaged from three locations on each transect
	Burn severity	RdNBR	Landsat TM+ satellite-derived relativized differenced normalized burn ratio (data from Dillon et al. 2011)
	Seed source	Distance PSME (m)	Mean distance to the nearest live Douglas-fir seed trees, measured from the center of each transect
		Distance PIPO (m)	Mean distance to the nearest live ponderosa pine seed trees, measured from the center of each transect

Note: Models contained at least one variable from each category, and each of the explanatory variables was required to be independent from one another.

† All climate variables are derived from 800-m resolution downscaled datasets and were averaged over the 30-yr period from 1981 to 2010.

including antecedent precipitation and annual water deficit (Table 1; Appendix S1: Table S1). We also included variables that represented post-fire conditions that were likely to affect the post-fire microenvironment and burned patch size (Table 1). We included the logarithm of sampling area as an offset variable in each of the models to account for our variable sampling area.

We developed a suite of candidate models that included all possible variable combinations of uncorrelated variables, with at least one variable from each category (i.e., temperature, precipitation, and fire severity; Table 1; Appendix S1: Table S1). We tested each of the explanatory variables for collinearity and excluded any variables that were well correlated (i.e., Pearson's  $|r| > 0.6$ ) from our candidate models. Fourteen possible models were constructed for both Douglas-fir and ponderosa pine, and each candidate model was fit with a negative binomial distribution (Appendix S1: Table S1), which accounted for the high overdispersion present in our tree seedling data. Of the 14 candidate models, we selected a final model based on Akaike's information criterion (AIC), explained deviance, and assessment of residual plots (Appendix S1: Table S1). We tested for assumptions of concurvity following the procedures outlined in Zuur et al. (2009).

To minimize dispersion in model residuals, we removed outliers and log-transformed variables displaying non-normal residual patterns. We also checked for spatial and temporal correlation among the sites in our data and added random effects to account for the different residual variance among plots (Zuur et al. 2009),

depending on the year of sampling (referred to herein as "time since fire") or the fire event within which the plots were sampled. All potential interaction terms were added to each model one at a time to see whether they improved model fit. Interaction terms that improved model fit were added to the final model.

We developed each of our final candidate models with all possible explanatory variables and interaction terms, and we subsequently reduced the model with a backward-stepwise selection procedure using AIC and a chi-squared analysis of deviance to assess model fit until the model contained only significant terms (Zuur et al. 2009). Final models were implemented with a tensor product smoothing function (Hastie and Tibshirani 1990, Wood 2006) using the *mcgv* (Wood 2011) and *MASS* (Venables and Ripley 2002) packages in R version 3.2.3 (R Development Core Team 2015).

Models were developed using historical climate data and observed tree seedling counts measured at each of our sampled sites; we then applied the models to predict current and future seedling counts using current and future climate projections. To test model reliability for making accurate predictions outside of the calibration dataset, we compared the sampled seedling counts to those predicted by the models using Spearman's rank correlation (Table 2). We cross-validated the models by randomly withholding 75% of the data to train the model and used the remaining 25% of the data for model validation for each of 1000 bootstrapped model runs. Cross-validation statistics and the Spearman's rank

Table 2. Summary statistics of model fit for full and cross-validated negative binomial generalized additive mixed models.

Statistic	Douglas-fir			Ponderosa pine		
	Full model	Cross-validation		Full model	Cross-validation	
		Mean	95% CI		Mean	95% CI
Explained deviance (%)	57.90	58.00	52.0–63.4	54.30	54.10	45.3–62.2
$\chi^2$ GOF statistic	1.02	1.02	0.98–1.06	0.56	0.56	0.50–0.63
$\chi^2$ P-value	0.43	0.42	0.30–0.55	1.00	1.00	1.00–1.00
Spearman's $\rho$	0.81	0.76	0.61–0.87	0.50	0.11	–0.15 to 0.34

*Notes:* We used a chi-squared goodness-of-fit test to examine the fit of the negative binomial distribution to the distribution of our data, where the null hypothesis assumes the model and empirical data come from the same distribution. A failure to reject the null hypothesis indicates a good fit of the model to the data. Spearman's rank correlation was used to assess the correlation between the predicted and observed seedling densities. Cross-validation was accomplished through 1000 bootstrapped model runs using 75% of the data to train the model and the remaining 25% of the data for model validation. Model means and 95% confidence intervals (CI) are reported.

correlation coefficient were summarized from each of the bootstrapped samples (Table 2).

We quantified changes in seedling densities at each of our sites under projected climate change by comparing predicted seedling densities from our initial models to densities predicted using future climate data. We used seedling density for this analysis, calculated by transforming count estimates to density based on transect area, because it is more generalizable than counts. We expressed changes in seedling densities as a percentage relative to our current model predictions (i.e.,  $[\text{future} - \text{current}] / \text{current} \times 100$ ), where positive values indicate predicted future increases in seedling densities and negative values indicate predicted future decreases. We considered sites where predicted future seedling density was within  $\pm 5\%$  of the current density to have no change, recognizing that small changes in predicted values are expected, independent of directional climate change. Finally, to identify where climate will likely be more suitable for tree regeneration under mid-21st century climate projections (RCP 8.5), we compared the elevation of sites where seedlings currently exist to the elevation of sites where seedling densities are predicted to increase (by more than 5%).

## RESULTS

Of the 177 sites sampled, 64% had Douglas-fir and 31% had ponderosa pine seedlings present. Although seedling densities varied widely (e.g., Douglas-fir: 0–68000 trees/ha; ponderosa pine: 0–1833 trees/ha), our final GAMMs explained 57% of the variability in the density of Douglas-fir and 54% of the variability in ponderosa pine seedlings using climate and fire variables alone. The addition of random effects and interaction terms improved overall AIC, residual patterns, and explained deviance with the least amount of additional terms for both species (Table 2). Cross-validation and a chi-squared goodness-of-fit tests confirmed the fit of a negative binomial distribution to our data (Table 2), and relatively high correlation between the predicted and observed seedling densities for both species suggests an ability to accurately predict Douglas-fir ( $\rho = 0.81$ ) and ponderosa pine ( $\rho = 0.50$ ) seedling densities (Table 2).

Mean summer temperature and distance to a live seed source were the most important determinants of Douglas-fir seedling density. Seedlings

were most likely to be found on sites with a mean summer temperature near 15°C. At sites with colder (i.e., below 11.2°C) and warmer (i.e., above 17.5°C) mean summer temperatures, predicted Douglas-fir seedling densities decreased (Fig. 2c). Estimated counts of Douglas-fir seedlings also decreased with distance to live seed source ( $\beta = -1.06$ ,  $P < 0.001$ ; Fig. 2a) and live tree stand density ( $\beta = 0.00$ ,  $P = 0.01$ ; Fig. 2a). Additionally, the interaction between summer temperature and distance to a live seed source significantly influenced the regeneration response in the final model (AIC = 1088.10; Appendix S1: Table S2). For example, when the distance to a live seed source was less than approximately 100 m, temperature played a strong role in determining how many seedlings regenerated; in contrast, when distance to seed source was greater than approximately 100 m, our model predicted lower seedling densities regardless of temperature (Fig. 3a). Likewise, our model reveals a temperature threshold, beyond which the distance to seed source has little influence on predicted Douglas-fir abundance: Above a mean summer temperature of 17°C, predicted Douglas-fir seedling densities are low (<90 trees/ha) regardless of how close a seed source was to the site (Fig. 3a).

Mean summer temperature was also an important driver of ponderosa pine densities and was the only main effect that remained significant in the ponderosa pine model after stepwise reduction. No interaction terms significantly improved model fit (AIC = 529.89; Appendix S1: Table S3). The relationship between summer temperature and ponderosa pine seedling count was similar to that of Douglas-fir: Predicted seedling densities were highest at a mean summer temperature of 14.8°C (Fig. 2d), with a slightly higher summer temperature range below/above which densities decreased (between 12.3°C and 18.5°C, respectively; Fig. 2d). There also appears to be a temperature threshold for ponderosa pine regeneration, though the effect is slightly less pronounced than with Douglas-fir (Fig. 3b). Ponderosa pine seedling densities are predicted to be low on sites with a mean summer temperature above approximately 19°C.

Informing our models with future climate data highlights change in the potential for seedling regeneration after future fires. Currently, a small proportion (19%) of sites that we sampled have a mean summer temperature exceeding 17°C, and of



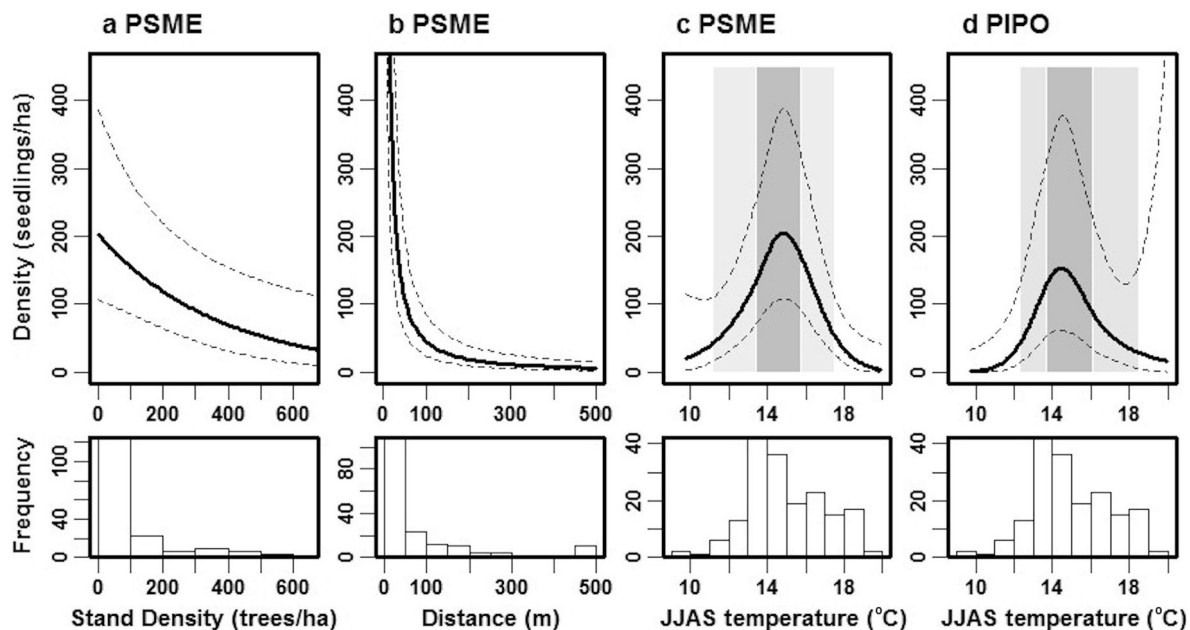


Fig. 2. Partial dependence plots showing the effect of the explanatory variable on the expected density of Douglas-fir and ponderosa pine seedlings while all other variables in the model are held constant at their medians. For Douglas-fir (PSME), (a) live tree stand density, (b) distance to a live Douglas-fir seed tree, and (c) mean summer temperature were the most significant variables predicting seedling density. For ponderosa pine (PIPO), (d) mean summer temperature was the only variable significantly influencing seedling density. In panels (c) and (d), the dark shaded area indicates the temperature range of 50% of the data under the fitted curve and the light shaded area 95% of the data. Dashed lines represent the 95% confidence intervals around the response. Histograms in the bottom row display the distribution of site data used to develop the generalized additive models. We expect wider confidence intervals where there were fewer sites sampled in any given data bin across the distribution.

those warmest observed sites, less than half (44%) contained one or more seedling of either species. By contrast, 78% of sites found in the 14–16°C temperature range had seedlings present. By the middle of the 21st century, based on the RCP 8.5 projections, 82% of the sites we sampled are projected to have a mean summer temperature greater than or equal to 17°C (Fig. 3c), implying that over three quarters of the sites we sampled across the range of dry mixed-conifer forests are likely to have lower potential for Douglas-fir (77%) and ponderosa pine (76%) regeneration, while only 22% and 10% of sites with Douglas-fir and ponderosa, respectively, were predicted to support higher seedling densities in the future (Fig. 4). Prior to fire, density of mature Douglas-fir ranged up to 754 trees/ha and up to 181 trees/ha for ponderosa pine, yet future seedling densities are predicted to be reduced below 294 and

126 trees/ha for Douglas-fir and ponderosa pine, respectively, on 90% of sites.

Given the strong dependence of seedling densities on temperature, sites projected to experience an increase in seedling densities occur within the highest elevations (>50th percentile) of sampled sites where ponderosa pine and Douglas-fir currently exist and where summer temperatures are currently suboptimal (e.g., <14°C; Fig. 5). Compared to the median elevation of sites where Douglas-fir and ponderosa pine are found today, sites predicted to support more seedlings in the future are 155 and 346 m higher, respectively (Fig. 5).

## DISCUSSION

Our results underscore the importance of both fire and climate in influencing post-fire seedling



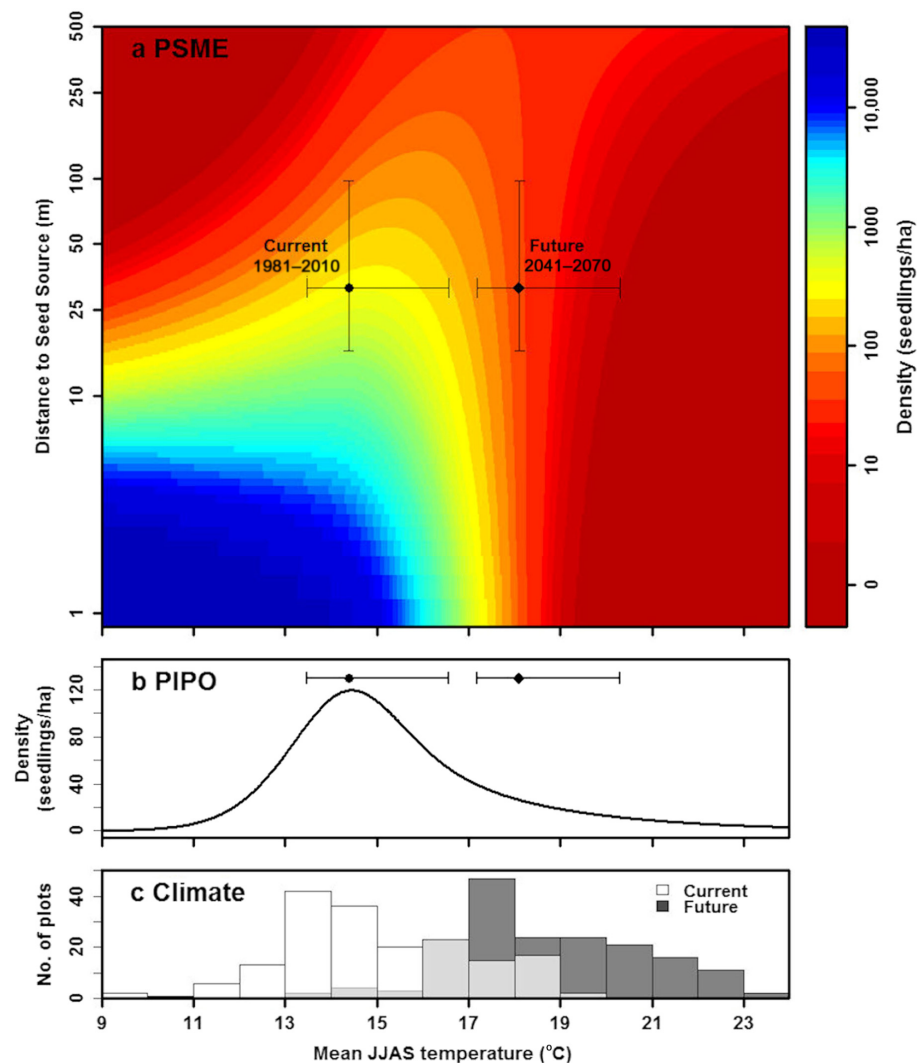


Fig. 3. (a) Contour plot showing predicted Douglas-fir (PSME) seedling densities for a range of different temperatures and distances to live seed source, (b) predicted ponderosa pine (PIPO) seedling densities across a range of different temperatures, and (c) the number of plots in each current (white) and predicted future (dark gray) temperature bin with overlap between current and future temperatures displayed by in light gray. Points in (a) and (b) represent the current and future median summer temperature at our sample sites based on CMIP5 RCP 8.5 model mean projections for the period 2040–2070. Whiskers extend to encompass the 25th and 75th percentiles of the data. For panel (a), whiskers also extend to encompass the interquartile range (50th percentile) of median distances to live seed trees. Most of our sites ranged between 20 and 100 m from a live seed source and had mean summer temperatures between 14°C and 17°C. At short distances to a live seed source, temperature was less of a determining factor of Douglas-fir regeneration. Likewise, at higher mean summer temperatures, distance to a live seed tree was no longer influential on Douglas-fir regeneration, suggesting biophysical thresholds for regeneration imposed by both climate and seed availability. CMIP5, fifth Coupled Model Intercomparison Project; RCP, Representative Concentration Pathway.

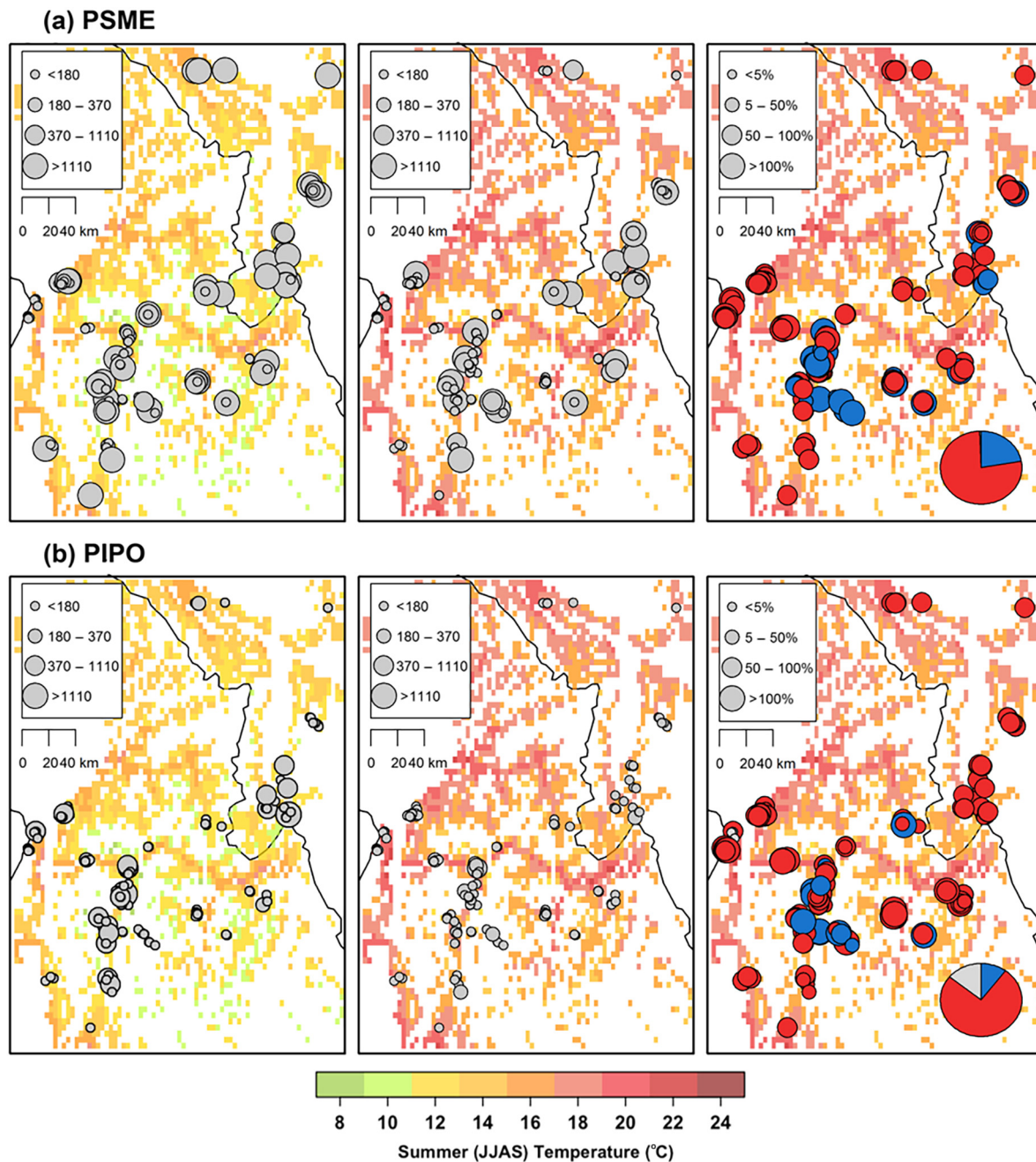


Fig. 4. Map of current (left), predicted future (center), and change (right) in (a) Douglas-fir (PSME) and (b) ponderosa pine (PIPO) seedling densities. The background in each map is the average summer temperature of dry mixed-conifer forest currently (1981–2010; left column) and as predicted for mid-century (2041–2070; center and right column) under the Representative Concentration Pathway 8.5 scenario. Seedling densities are considered to have changed if the density increased or decreased by at least 5% over the predicted period. Pie charts display the percent of sites with increase (blue), decrease (red), and no change (gray) for each species.

regeneration in dry mixed-conifer forests. Further, they allow us to assess the relative importance of each factor in shaping present and future forest composition. Complex interactions between fire and climate varied by species, implying that the impacts of future climate change and disturbances may not just alter species extent but also forest composition as species respond individually to different stressors. Likewise, the role of fire in mediating responses to climate will change through time as temperatures increase.

#### *Climate and fire interact with species' traits to shape patterns of forest regeneration*

Post-fire regeneration patterns of Douglas-fir and ponderosa pine were influenced by different variables. Douglas-fir regeneration was linked with both climate and fire-related variables, such

as distance to a live seed tree and post-fire live tree density. Conversely, our models indicated that ponderosa pine regeneration was influenced solely by mean summer temperature. This finding is consistent with the differences in the ecology and climatic niche of these two species: Ponderosa pine displays less phenotypic plasticity than Douglas-fir and has been shown to be more vulnerable to climate change scenarios (Rehfeldt et al. 2014a, b). This higher sensitivity to climate may explain why climate outweighed other factors in the final statistical model predicting ponderosa pine seedling abundance. In contrast, Douglas-fir occurs over a broader climate gradient than ponderosa pine, which may explain why other biophysical factors were useful in predicting post-fire seedling abundance. These species-specific differences will shape future patterns of forest

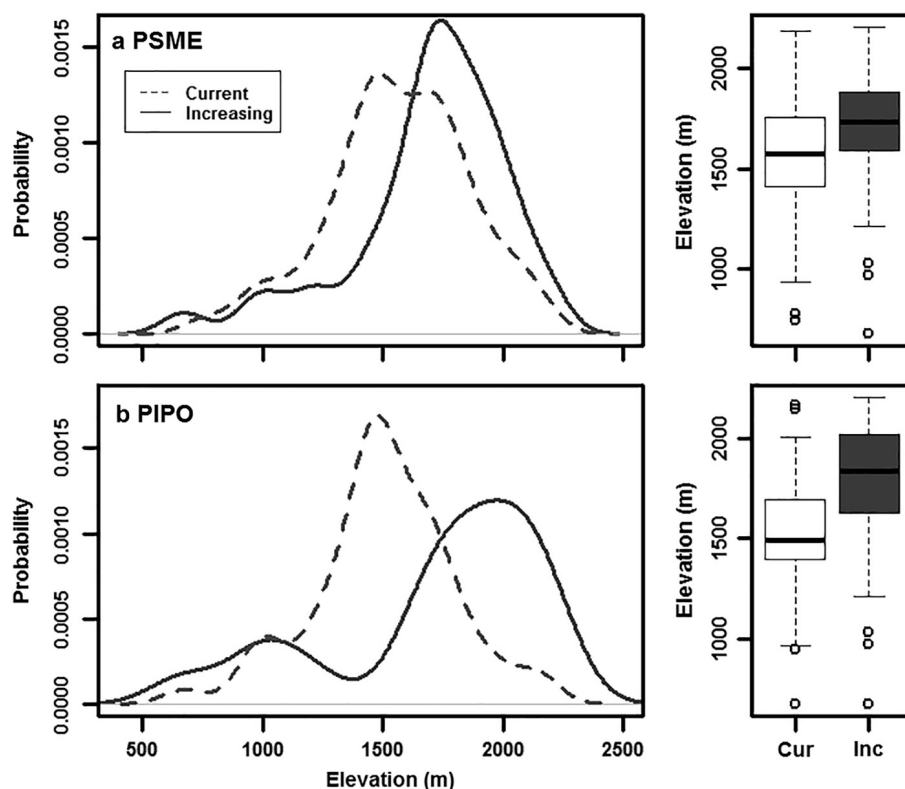


Fig. 5. Probability density functions for the elevation of sites where seedling densities are predicted to increase (solid line) relative to current (dashed line) modeled densities for (a) Douglas-fir (PSME) and (b) ponderosa pine (PIPO). Sites were defined as having increasing densities if there was at least a 5% change between the predicted current and predicted future seedling densities. Boxplots show the 25th, 50th, and 75th percentiles, and whiskers extend to the 5th and 95th percentile elevation of sites where seedlings of each species are currently present and predicted to increase in the future. Circles represent outlier sites.

regeneration and may make it challenging to quantify how dry mixed-conifer forests will respond to future fires and a warming climate.

While different variables were important in predicting each species' regeneration potential, mean summer temperature was an important indicator of regeneration success after fire for both Douglas-fir and ponderosa pine. Although we sampled a full range of sites characterizing dry mixed-conifer forests, we observed far fewer Douglas-fir and ponderosa pine seedlings on sites with the warmest mean summer temperatures; with warmer mean summer temperatures, the potential for successful regeneration decreased (Fig. 2c, d). Year-to-year variability and temperature extremes are likely to also be critically important to the success of post-fire regeneration (Rother et al. 2015, Petrie et al. 2016), especially in the early stages of seedling establishment when seedling survival is vulnerable to drought and excessive heat (Kolb and Robberecht 1996). Yet, as fewer optimal post-fire climate windows occur, average site climate conditions may increasingly determine the success or failure of post-fire regeneration (Stevens-Rumann et al. 2018).

In areas burned at high severity, tree mortality contributes to lower seed availability (Savage and Mast 2005, Haire and McGarigal 2010, Kemp et al. 2016), but fire effects can also create mineral seed beds and free up resources such as light, water, and nutrients that facilitate tree recruitment (York et al. 2003, Gray et al. 2005, Moghaddas et al. 2008). Douglas-fir regeneration appeared to be responding to the tradeoffs between seed availability and resource availability in our study, though distance to a live seed tree had a much stronger effect on potential regeneration (Fig. 2b). Few Douglas-fir seedlings were present on sites where live seed trees were more than 100 m away, consistent with established dispersal distances of Douglas-fir seeds (McCaughy et al. 1986). Likewise, when the density of live mature trees exceeded 200 trees/ha, regeneration of Douglas-fir was lower (Fig. 2a). Fire-created canopy openings may have increased resources and reduced competition, thus improving the suitability of some sites for post-fire tree regeneration (York et al. 2003). In contrast, distance to seed source was not a significant predictor of ponderosa pine seedling density. As seeds are clearly required for

regeneration (highlighted in these same study plots and by others; e.g., Bonnet et al. 2005, Donato et al. 2009, Kemp et al. 2016 [which did not include climate as a potential predictor], Stevens-Rumann et al. 2018), this finding suggests that when seedlings are present, the number of successful germinants is driven more by growing season climate than distance to seed source. This also indicates that different variables may be important for predicting seedling presence or absence versus predicting seedling density.

Our work further highlights that as temperatures warm, the relative influence of wildfire will change. Currently, fire plays an important role in determining post-fire regeneration through its influences on tree mortality and seed availability (Chambers et al. 2016, Harvey et al. 2016, Kemp et al. 2016). As climate continues to warm, post-fire forest structure may have little influence on tree regeneration as regeneration becomes overwhelmingly determined by climate (Stevens-Rumann et al. 2018). For example, for Douglas-fir, once mean summer temperatures exceed a critical threshold, seedling regeneration is projected to be low regardless of seed availability: Near-by seed sources are necessary but not sufficient for successful germination. Our results suggest that the influence of fire under future warming may increasingly be limited to its role in causing tree mortality, rather than also influencing post-fire regeneration through seed availability. It remains unclear how the loss of forest canopy cover, which can moderate temperature extremes at the seedling scale (Dobrowski et al. 2015; Davis et al. 2019), may amplify the impact of a warming climate on seedling regeneration.

#### *Climate warming will increasingly determine tree regeneration*

Although summer temperature was an important driver for both ponderosa pine and Douglas-fir abundance, future temperature increases will differentially affect these two species. Our models indicate that Douglas-fir regeneration is unlikely in areas where the mean June–September temperature exceeds 17°C, regardless of whether seed sources were available. By mid-century, the majority (82%) of sites that we sampled, which represent the range of dry mixed-conifer forests in the Northern Rockies across latitudes and elevations, are projected to be above that temperature



threshold for seedling survival, leading to significant projected decreases in Douglas-fir regeneration. The slightly higher temperature tolerance of ponderosa pine results in a higher likelihood of regeneration at sites at or above 17°C; however, seedling survival of ponderosa pine will also be compromised in a warmer future climate (Petrie et al. 2017). The temperature thresholds that emerge from this work are specific to our study region (Figs. 1, 3c), as we studied ponderosa pine and Douglas-fir across only a small portion of their geographic ranges (Rehfeldt et al. 2014a). We would expect to find other temperature thresholds in other regions of western North America, based on biophysical differences including taxonomic varieties and seasonality in precipitation and temperature.

As the climate continues to warm, higher-elevation sites are projected to become more favorable for both ponderosa pine and Douglas-fir regeneration (Fig. 5), suggesting regeneration of these two species may shift upslope in the future, potentially shifting lower treeline upslope in areas where few trees survive recent fires. This pattern has been observed in dry mixed-conifer sites in eastern Oregon, where post-fire regeneration increased with elevation (Dodson and Root 2013). Currently, ponderosa pine occurs at a lower median elevation than Douglas-fir and may replace Douglas-fir at mid-elevation sites. Likewise, north-facing aspects with less solar insolation were associated with greater tree regeneration after fire for several conifer species on xeric sites in Colorado (Donnegan and Rebertus 1999). As climate continues to warm, we expect that post-fire tree regeneration will become increasingly constrained to locations where topography moderates the effects of an overall warming climate.

Although our models reveal the strong impacts of climate, and specifically summer temperature, on seedling regeneration, our ability to infer the specific mechanisms linking climate to successful regeneration is inherently limited. We expected water balance variables that are more closely tied to tree physiology, such as AET, PET, and water deficit, to be important, but they were not included in our final models. We suspect that our models may underrepresent the importance of these metrics for ponderosa pine and Douglas-fir. While downscaled temperature data are determined by physical relationships with

elevation, which are often modeled at fine scales (e.g., 10-m digital elevation models), the methods by which AET, PET, and soil data are modeled in mountainous regions could lead to compounded uncertainties that may not sufficiently capture the fine-scale variability that contributes to the energy and water constraints experienced by tree seedlings. Further, calculations of AET, PET, and water deficit use estimates of water demand from a standard reference crop, but transpiration rates of conifer seedlings are likely to make them much more tolerant of lower soil water availability and desiccation relative to reference crops (Fowells and Kirk 1945). Finally, we used climate normals to project future seedling densities, but seedlings are likely to respond to climate variability as well as average conditions, which we did not include as predictor variables in our models. If favorable climate windows coincide with seed availability, they may provide regeneration opportunities even on unfavorable sites (Stevens-Rumann et al. 2018).

#### *Implications for forest resilience to climate change*

Forests in the U.S. northern Rockies have been relatively resilient to large-scale fires over the past several decades (Kemp et al. 2016) and centuries (Heyerdahl et al. 2008). As climate warms, however, the ability of fires to catalyze large-scale vegetation change at site and landscape scales is increasing (Stevens-Rumann et al. 2018). The combination of increased tree mortality from fire and less tree recruitment due to less-favorable climate conditions (Andrus et al. 2018, Stevens-Rumann et al. 2018) is likely to result in shifts in forest extent and composition (Enright et al. 2015). Where there is a mismatch between recruitment potential and mature adults, the regeneration niche will determine patterns of species occurrence, abundance, and recovery following disturbance (Jackson et al. 2009, Dobrowski et al. 2015). Dry mixed-conifer forests of the U.S. northern Rockies occupy a broad temperature range, but our research indicates that the optimal climate niche for seedling regeneration of both Douglas-fir and ponderosa pine occurs at locations with a mean summer temperature between 14°C and 16°C. This suggests that while mature individuals that survived recent fires may continue to persist on some sites, few trees will successfully regenerate, especially at low elevations or on the

warmest, driest sites in the region. As landscapes continue to warm in the future, the potential for a conversion to non-forest may occur where most mature trees are killed by wildfire and regeneration is limited or fails altogether, resulting in an upslope shift in lower treeline.

Our findings that climate and fire interact to influence seedling regeneration have important implications when considering the impacts of future fire regimes under a warming climate. Repeated fires at short intervals may remove mature and juvenile trees that could have provided seed sources for subsequent tree regeneration (Keeley et al. 1999, Brown and Johnstone 2012). Likewise, if the relative size of high-severity patches increases with future climate change, and more areas experience stand-replacing fires, the removal of seed sources could limit future regeneration (Harvey et al. 2016, Kemp et al. 2016). Although we did not quantify the impacts of increased fire extent and burn severity on seedling regeneration in the future, fire extent is projected to increase two- to fivefold by mid-century in the U.S. northern Rockies (Littell 2011), which would lead to more area burned at high severity even if the proportion of area burned severely does not increase (Dillon et al. 2011). The interactions between increased area burned, more patches of stand-replacing fire, and repeated fires will therefore have important implications for future forest structure and composition (Johnstone et al. 2016).

Maintaining forest resilience to climate change and increased fire activity is a high priority for forest managers (Kemp et al. 2015) and a key focus of the National Cohesive Wildland Fire Management Strategy (USDOI and USDA 2014). Understanding where the landscape may or may not be able to support the regeneration and survival of valued tree species will help forest managers prioritize management strategies for conserving future forests. The establishment or planting of trees in areas recovering from recent disturbances may help slow the projected impacts of climate change, as trees that establish under suitable conditions in the present may be less likely to succumb to warmer temperatures in the future. Likewise, if sustaining forests cover of early seral dry mixed-conifer forest species is high priority, forest managers may continue to use fuels treatments, including thinning and prescribed fire, to reduce the likelihood of extensive

patches of high tree mortality in future large fires (Martinson and Omi 2013, Kalies and Kent 2016). Maintaining extant seed sources and encouraging persistence of fire-resistant species will help reduce the potential for a shift in forest extent, species composition, or abundance, and increase the likelihood that forests are resilient to future disturbances (Johnstone et al. 2016).

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## DATA AVAILABILITY

Code and datasets associated with this manuscript are available at the Dryad Digital Repository (<https://doi.org/10.5061/dryad.9g91451>).

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2568/full>